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The effect of age on interhemispheric transfer time: an event related potential study

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Abstract

The present study sought to investigate the effects of aging on interhemispheric transfer time (IHTT). Poffenberger (1912) devised a behavioural paradigm thought to be a measure of IHTT. In this paradigm IHTT is estimated by calculating the crossed-uncrossed difference (CUD); the difference in speed of response between responses made in response to stimuli contralateral to responding hand (crossed) and those made by hands ipsilateral to the stimuli (uncrossed). IHTT can also be estimated through event related potentials (ERPs) by calculating latency differences between the waveforms over the ipsilateral and contralateral hemispheres. Results from previous experiments comparing younger and older participants with these two methods are inconsistent. Twenty three younger (18-25 years) and 23 older (65-77 years) participants had their electroencephalogram (EEG) recorded whilst completing the Poffenberger paradigm. IHTT estimates from the two measures were compared between the groups. Older participants were found to have a faster IHTT estimate from the P1 ERP component compared to younger participants. This result is in contrast to the current literature. Replication of this result is recommended before firm conclusions about its implications can be made.

Introduction

The brain has been shown to go through many changes during normal aging, with effects on brain activation and functioning (Banich & Compton, 2011; Grady, 2008; Raz, 2005). Understanding what happens to the brain during the normal aging process is important in order for these effects to be distinguished from those of disease patterns (Bennett, Madden, Vaidya, Howard, & Howard, 2010; Ge, et al., 2002). The more that is known about these changes, the more understanding can be gained for the potential deficits which might manifest themselves throughout the aging process in the normal population. One such area of interest is how well the two hemispheres integrate and process information. The time it takes for information to transfer from one hemisphere to the other is one aspect of this process.

Interhemispheric Transfer Time (IHTT) and its Measurement

Poffenberger (1912) described a simple behavioural paradigm which is thought to be a measure of interhemispheric transfer time (IHTT). Participants are required to respond to a stimulus presented in either the left or right visual field for a matter of milliseconds (ms) with either their left or right hand (see Figure 1). When the responding hand is contralateral (opposite) to the presented stimulus, reaction times are longer than when the responding hand is ipsilateral (on the same side); a finding which has been widely replicated (Marzi, Bisiacchi, & Nicoletti, 1991). This is thought to occur because sensory information is received by one hemisphere but the response is required from the other which involves the sharing of information between the hemispheres. IHTT is estimated by calculating the crossed-uncrossed difference (CUD); the difference in speed of response between the crossed (contralateral) and uncrossed (ipsilateral) hand/hemifield conditions.

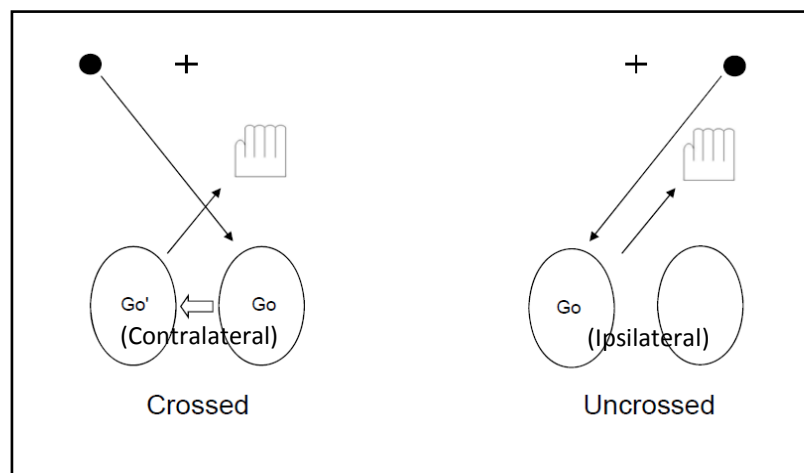


Figure 1: The crossed and uncrossed conditions of the Poffenberger paradigm showing the transfer of visual information across the hemispheres in the crossed but not uncrossed condition.

The anatomical model on which the CUD is based is a basic one, relying on only a single visuomotor pathway (Saron, Foxe, Simpson, & Vaughan, 2003). The retina of each eye is split into two hemifields; those located to the right (left nasal and right temporal) capture the left visual field (LVF) and project to the right hemisphere; those located to the left (right nasal and left temporal) capture the right visual field (RVF) and project to the left hemisphere. This means that information can be presented to one visual field and only be transmitted to one hemisphere of the brain (Purves, et al., 2008). Distal effectors such as fingers show the same pattern of organisation, being almost exclusively controlled by the contralateral hemisphere; fingers of the left hand are controlled by the right hemisphere and vice versa. In the crossed condition of the paradigm visual information is received by one hemisphere while the specified response is required from the other; the uncrossed condition does not require such transfer of information as the stimulus input and motor response are both processed by the same hemisphere (Zaidel & Iacoboni, 2003). The difference in reaction time (CUD) is therefore thought to represent the time taken to transfer information across the CC to the responding (ipsilateral) hemisphere (IHTT).

A meta-analysis of data from over 300 participants has yielded a typical transfer time of about 4 ms (Marzi, et. al., 1991). Marzi, et al. (1991) also note an asymmetry of transfer with right-to-left hemisphere faster than left-to-right. The CUD increases significantly in acallosal (Rugg, Milner, & Lines, 1985) and callosally sectioned patients (Aglioti, Berlucchi, Pallini, Rossi, & Tassinari, 1993; Brown, Bjerke, & Galbraith, 1998), suggesting it is in fact the corpus callosum (CC) which mediates the process. Corballis, Corballis, and Fabri (2003) suggest that it is specifically the posterior CC which facilitates the rapid transfer of stimulus information in simple reaction time tasks, such as the Poffenberger paradigm. The CUD is also independent of the stimulus-response compatibility effect; when participants' arms are crossed, responses are still faster with the hand anatomically ipsilateral to the visual stimulus (Anzola, Bertoloni, Buchtel, & Rizzolatti, 1977). Manipulation of the visual parameters of stimuli does not affect the CUD (Braun, 1992; Corballis, 2002) suggesting that it is not visual sensory information transferred but motor information related to response selection (Basso, et al., 2006; Corballis, 2002; Milner & Lines, 1982) or decision making (Corballis, 2002).

Evidence suggests that handedness can affect IHTT. Some studies have found that left handed participants produce a shorter CUD than right handers, although this difference was not statistically tested (Jeeves, 1969; Jeeves & Dixon, 1972). Other research reviewed by Saron, et al. (2003) highlights left handers having negative CUDs. Cherbuin and Brinkman (2006a; 2006b) looked at IHTT and interhemispheric interaction (IHI) and found that they were positively correlated in both left- and right-handed participants, but left-handers showed more efficient hemispheric interactions (Cherbuin & Brinkman, 2006b). Bernard and Seidler (2008) found significant differences between CUDs of left and right handers, such that left-handed participants produced significantly faster CUDs. These studies are consistent with anatomical evidence suggesting the left-handers may have increased interhemispheric connectivity (Westerhausen, et al., 2004).

IHTT can also be estimated through the use of visual event related potentials (ERPs). ERPs refer to aspects of electrical potential within the electroencephalogram (EEG) recording which are time locked to specific events, such as stimulus onset, which then provide insight into the timing of processing in the brain (Banich & Compton, 2011). ERPs are considered to represent the summed electrical activity of neurons specifically responding to these events (Purves, et al., 2008), and as such are conceptualised as manifestations of psychological processes (Fabiani, Gratton, & Coles, 2000). When measuring IHTT, recordings are made simultaneously from homologous sites over each hemisphere of the brain activity evoked from stimulus input to only one hemisphere. IHTT is estimated using latency differences between the ERP components from the homologous sites (Brown, et al., 1998; Saron & Davidson, 1989). For example, a stimulus presented to the LVF initially produces an ERP component over the contralateral right hemisphere. Stimulus information is then transferred via the CC and a resulting ERP can be detected over the ipsilateral left hemisphere. IHTT is taken as the difference in the time taken for the ERP to appear in the right compared to the left hemisphere (Brown, et al., 1998). Asymmetry of transfer can also be seen with ERP measures; transfer is faster in the right-to-left direction (Barnett & Corballis, 2005). ERP derived IHTT has been found to be between 8 and 19ms (Saron & Davidson, 1989; Westerhausen, et al., 2006; Whitford, et al., 2011) which is much longer than the 4ms estimates from the CUD measure. This implies that the two measures might be measuring different processes which led to Saron and Davidson (1989) questioning the validity of the CUD as a measure of IHTT.

CUD versus ERP Measures of IHTT

The simple paradigm introduced by Poffenberger is a behavioural measure based on reaction times (RTs). Saron and Davidson (1989) note that the only type of callosal axon able to mediate the short IHTTs found with this measure would need to be large in diameter (2.5-6 μm) and myelinated; such axons account for only 10% of fibres in the brain. Further, over half the myelinated axons of the CC are narrower than 1.5 μm which together gives a reason to doubt the methodology of the CUD as a valid measure of IHTT (Saron & Davidson, 1989). Iacoboni and Zaidel (2000) provide support for this conclusion. In their study intra- and inter-subject CUDs were calculated and a large variability was found within-subjects which did not differ from that of between-subjects. It was concluded that inter-subject variability in the CUD does not reflect reliable between-subject differences and as such the CUD is an unstable measure of IHTT.

Saron and Davidson (1989) directly compared CUD and ERP derived measures of IHTT. Predictions for IHTT state that the results should be significantly different from zero with positive values indicating increasing time (Saron & Davidson, 1989). Negative values would indicate that crossed conditions were completed faster than uncrossed; an anatomical impossibility if information must cross between the hemispheres. Results showed that ERP measures provided results in the anatomically predicted direction more reliably than CUD measures and as such it was concluded that ERPs are the more valid measure. Another finding of this study was that the two measures were uncorrelated, further suggesting that they measure different processes. Saron and colleagues (2003; 2004) note that bilateral frontal, central, and occipital activation before

or during motor response in the uncrossed conditions is evident, which violates the paradigm's assumption that processing in this condition is contained within the one hemisphere. Bilateral activation was also found by Iacoboni and Zaidel (2004) in prefrontal and dorsal premotor areas, as well as unilateral activation of superior parietal areas. They concluded that multiple transfers occur in parallel related to sensory-motor integration, decision-making and motor response preparation. This conclusion is contrary to the assumption of the CUD relying on a single visuomotor pathway. It has also been suggested that RT in this paradigm is related to the rate of premotor activation rather than the timing of movement onset (Saron, et al., 2003; 2004). This is consistent with the suggestion by Kinsbourne (2003) that lateral processing takes place only after interhemispheric transfer and that the CUD is only a reflection of the time taken for neurons to reach activation threshold and not callosal transfer.

The Aging Corpus Callosum

The corpus callosum (CC) is the largest white matter (WM) tract connecting the two cerebral hemispheres with over 200 million axons (Ota, et al., 2006). It plays a crucial role in the integration of sensory, motor, and cognitive information (Reuter-Lorenz & Stanczak, 2000). A topographic organisation of the CC is usually assumed but Clarke (2003) states that this has only been confirmed for anterior parts of the frontal lobe which cross areas of the genu (anterior CC), and for occipital cortex axons which pass through the lower splenium (posterior CC). The results of volumetric studies into the effect of age on the size of the CC are inconclusive; some studies find a reduction (Sullivan, Pfefferbaum, Adalsteinsson, Swan, & Carmelli, 2002), while others do not (Pfefferbaum, et al., 2013). The structural integrity of the CC has been shown to decline with age even when volume declines are not necessarily detectable (Sullivan & Pfefferbaum, 2006). These declines are of importance to IHTT as subtle degradation of the CC influences the processes it is involved in (Schulte & Müller-Oehring, 2010).

Diffusion tensor imaging (DTI) measures the diffusion of water molecules, which is anisotropic (direction specific) in WM, allowing mapping of the WM tracts (Le Bihan, 2003). Sullivan and Pfefferbaum (2006) reviewed studies which examined the structure of WM including the CC and found an age related decline in fractional anisotropy (FA) which is thought to reflect reduced structural integrity. Ota, et al. (2006) found a reduction in FA in the genu and areas of the middle third of the CC, along with an increase in mean diffusivity which also indicates reduced structural integrity. Increased radial and axial diffusivity has also been found in the genu suggesting axonal damage or loss and demyelination (Burzynska, et al., 2010; Ota, et al., 2006). The genu of the corpus callosum contains many small diameter unmyelinated and thinly myelinated axons, the latter of which are highly susceptible to degeneration and demyelination with age (Bennett, et al., 2010). This could be the reason for the anterior-posterior gradient of degradation that is seen in both the CC (Burzynska, et al., 2010; Sullivan & Pfefferbaum, 2006) and cortical WM (Bennett, et al., 2010). This gradient suggests that the regions of the CC implicated by Corballis, et al. (2003) in the CUD might be the last regions to degrade with age.

IHTT and CC Degeneration

Consistent findings show that overall reaction times slow with age and this has been found to correlate with reduced structural integrity (van der Knapp & van der Ham, 2011). An additional functional consequence could also be an increase in IHTT (Sullivan & Pfefferbaum, 2006; Thompson, Narr, Blanton, & Toga, 2003). Sullivan and Pfefferbaum's (2006) review noted that an increased CUD was associated with low FA and high MD in the genu and splenium irrespective of the age of the participant. This suggests the microstructural integrity of the CC affects the efficiency of interhemispheric processing. Westerhausen et al (2006) provide support for this suggestion through their investigation of how IHTT is affected by individual differences in the architecture of the CC. It was found that FA was negatively correlated with the P100 component of the ERP derived IHTT. This was especially evident in the posterior CC sub-region which Corballis, et al. (2003) highlighted to be the region mediating the CUD. Whitford, et al. (2011) compared DTI with ERP IHTT and also found FA to be negatively correlated with IHTT. WM and the CC have been implicated in schizophrenia with regards to impaired connection between cortical regions (Kubicki, et al., 2007; van der Knapp & van der Ham, 2011). ERP derived IHTT data suggests that these patients have a longer IHTT in the left to right direction compared to normal controls (Barnett & Kirk, 2005; Endrass, Mohr, & Rockstroh, 2002). Such a finding in a patient group implies that a similar finding might be found in other population groups who show WM and CC degeneration, for example, in the aged population.

CUD and ERP IHTT with Age

Jeeves and Moes (1996) investigated the effect of aging on CUD derived IHTT. Their results showed that older participants had a significantly longer CUD compared to younger participants, suggesting a longer transfer time. However, they noted that the majority of this effect came from their older female participants, whereas the younger group showed no gender difference. This might suggest that aging affects the genders differently. Reuter-Lorenz and Stanczak (2000) compared two behavioural measures of hemispheric function: CUD IHTT and attentional resource allocation. They replicated the results of Jeeves and Moes (1996) of a longer transfer time in older participants but instead of possible gender differences, their results suggested that the extended CUD in older participants was primarily due to the right hand responses. The attention task showed no effect of age, from which the authors conclude that aging affects callosally mediated processes differently. Schulte, Pfefferbaum, and Sullivan (2004) also found that older participants had a longer CUD. This study compared CUD to callosal size and found a negative correlation such that longer CUDs were associated with a smaller CC, which is consistent with the structural integrity research. However, Linnet and Roser (2012) measured CUD in young and aged participants but found no differences between the two groups, indicating that there is no effect of age on the CUD.

Hoptman, et al. (1996) used CUD and ERP measures to compare IHTT of young and aged participants. Nearly identical methods to Saron and Davidson (1989) were used, including the use of checkerboard stimuli. A large difference in IHTT was evident using the two methods; RT CUD produced an IHTT of 2.1ms whereas the ERP data produced an IHTT of 23ms. No effect of age was found but a reduction in the quality of the signal

transferred was evidenced by a decrease in the amplitude of the ERP waveform over the ipsilateral hemisphere. The lack of age effects in the latency data could be a result of averaging of the latencies from both temporal and occipital electrode sites despite noting that the data implied IHTTs to be shorter at the temporal sites for the P100 component. Curran, Hills, Patterson, and Strauss (2001) conducted an ERP study to investigate the effects of age on visuospatial attention and found evidence which is consistent with age differences in IHTT. Their results suggest that aging slowed the latency of the ipsilateral but not contralateral P1 ERP component.

Both Jeeves and Moes (1996) and Reuter-Lorenz and Stanczak (2000) found age differences with the CUD measure but both highlight that their results could be due to other factors such as gender or response hand. Together with the lack of age differences in the Linnet and Roser (2012) study, this might mean the CUD is not a reliable measure of the effects of age on IHTT, which is in line with the conclusions of Saron and Davidson (1989). Currently there is no consensus on the effect of age on IHTT due to the mixed results found with both CUD and ERP measures. Saron and Davidson's paper implies ERPs are the better measure yet they are not reliably producing the expected results based on our current understanding of corpus callosum degeneration and its effect on hemispheric interaction (Sullivan & Pfefferbaum, 2006; Westerhausen, et al., 2006).

The Present Study

The present study investigated the effect of age on interhemispheric transfer in young and aged participants using both CUD and ERP measures. It was predicted that there would be a significant lengthening of IHTT with age. Only right handed participants were recruited for this study to eliminate the potential confounding variable of handedness. The stimuli used were a checkerboard pattern as per Saron and Davidson (1989) and Hoptman, et al. (1996). Following the recommendation of Saron and Davidson (1989), a linked mastoid reference was used for the ERP data as this was shown to be the more reliable over a frontally placed reference for IHTT measurement. Recordings were taken from occipital and parietal electrode sites with a further prediction that ERPs would be greatest over the occipital sites O1 and O2. Occipital and parietal sites were analysed separately to avoid the possible confounds of averaging over multiple sites as per the Hoptman, et al. (1996) study.

Methodology

Participants

Twenty five younger participants and 25 older participants gave informed written consent to take part in the study. Twenty three participants in each group provided data: one younger participant was suspected of epilepsy and therefore was not permitted to take part, technical difficulties with one younger and one older participant meant data could not be collected, and one older participant was left handed and as such their data not used. Younger participants ranged from 18-25 years old ($n=23$, $M = 19.91$, $SD = 1.70$) with 7 male and 16 female participants and were all undergraduate psychology

students participating for course credit. Older participants ranged from 60-77 years old ($n = 23$, $M = 68.3$, $SD = 3.98$) with 13 male and 10 female participants, and were paid for their time. Participants were required to have normal or corrected to normal vision, have no skin conditions or allergies, have no history of neurological symptoms, head injury, or haemophilia, or be taking any medication with neurological side effects.

All participants were administered a 12-item version of the Edinburgh Handedness Inventory (Oldfield, 1971) as a measure of handedness. Participants were required to have a laterality quotient to the right of zero, indicating right handedness. In addition, 20 of the 23 older participants were administered the Mini Mental State Examination (Folstein, Folstein, & McHugh, 1975) to screen for possible cognitive deficits which might affect the participant's task performance or understanding of the task. Due to technical difficulties in administration 3 participants were not screened on this measure. Participants were required to have a score greater than or equal to 26; the suggested cut off for normal performance and intact cognitive ability (Folstein, et al., 1975).

Procedure

Stimuli were presented via E-Prime software version 2.0 (Psychology Software Tools, 1996). Reaction time data via button press responses were recorded by a response box linked to this software. Participants were seated approximately 114cm from a 23" CRT display screen (Viewsonic P227f, set at 1024x768 resolution; 100Hz refresh rate) placed at eye level. Participants were instructed to make a speeded response to seeing flashed stimuli presented on either side of a fixation cross. They were instructed to maintain fixation with the cross at all times during the experiment. Responses were made with either the left or right thumb, with written instructions given on the screen prior to each experimental block as to which hand to use. Participants completed a set of practice trials to familiarise themselves with the procedure, after which any errors in response were addressed and the opportunity given for questions to be asked. The initiation of each experimental block was executed by the experimenter who monitored the EEG output as well as the participant themselves to ensure that the participant was relaxed and ready for the next trial. On completion of all 10 blocks, the participant was thanked for their time and debriefed. As per lab protocol, all participants were offered hair washing to remove the electrolyte gel.

Stimuli

Each stimulus comprised of a 3x3 checkerboard of black and white squares subtending 3.5° of visual angle (7cm horizontal distance) from a central fixation point. The checkerboard subtended 3.5° visual angle (7cm wide), with a height of 4.15° (8.3cm). Stimuli were displayed to the left or right of a black central fixation cross on a grey background for approximately 50ms. The fixation cross remained visible throughout stimulus presentation and for a variable stimulus-onset asynchrony (SOA) of 1000-2000ms after the stimulus disappeared to allow for the dissipation of brain electrical activity from the previous stimulus (Saron, et al., 2003). Following the SOA the next stimulus was displayed. The experiment was run in 10 blocks of 35 trials, 5 of which were catch trials where no stimulus was displayed but the time course remained the same. Such trials were included to again avoid expectancy effects, ensuring the

participants' responses were not anticipatory. Visual field of presentation was randomised within each block with equal numbers of presentations to the left and right; 15 trials to the LVF and 15 to the RVF.

Data recording

EEG data were collected from 13 actively amplified Ag/AgCl electrodes (actiCAP, Brain Products, Gilching, Germany) mounted on an elastic cap. The electrodes were Oz, O1, O2, Pz, P3, P4, P7, P8, TP9, TP10, RVa, RVb, and AFz (ground), based on the standard 10-20 montage. Electrodes were referenced to the left mastoid (TP9) and re-referenced offline to the average of left and right (TP10) mastoid activity. Eye movement was monitored by RVa and RVb electrodes placed lateral to and below the right eye. Inter-electrode impedances were kept below 20k Ω . EEGs were amplified using a BrainAmp amplifier (Brain Products), continuously sampled at 5000 Hz, with a low cut-off filter time constant of 10 seconds and a high cut-off filter of 1000Hz. A high cut-off digital filter was also applied at the time of recording of 30Hz. Trials with more than 30% artefact affected trials were excluded from analysis; rejection of EEG if electrodes RVa and/or RVb showed a voltage change of 80 μ V per 400ms within a pre-stimulus interval of 100ms and 200ms post-stimulus. In addition, those participants deemed to have excessive alpha wave activity were also excluded. This resulted in 15 younger and 14 older participants contributing data to the grand average waveforms. ERPs were calculated by averaging EEG time-locked to 100ms before the onset of the stimulus to 600ms after and were baseline corrected using the 100ms period prior to stimulus onset. Grand average waveforms were then calculated for each Visual Field x Electrode pair for both the P1 and N1 component.

Results

Reaction Time Data

Reaction times shorter than 100ms (anticipatory response) or over 500ms (delayed response) were excluded from analysis as outliers in the data. Means and standard deviations for reaction times by hand and visual field (VF) for both the younger and older participants are presented in Table 1, together with the crossed-uncrossed difference calculation for each VF. Statistical analysis was performed using a three-way analysis of variance (ANOVA) with Hand (left or right) and Visual Field (LVF or RVF) as the within-subjects factors and Age (younger or older) as the between-subjects variable. Assumptions of the ANOVA were not violated. There was a significant Hand x VF interaction, $F(1,44)=30.19$, $p<.001$, $\eta^2=.41$ indicating that uncrossed conditions produced a faster reaction time than uncrossed conditions for both Hand conditions. This produced a significant CUD in the anatomically predicted direction. However, this did not differ between the groups; Hand x VF x Group interaction was not significant, $F(1,44)=.75$, $p=.39$, $\eta^2=.02$. No other significant effects were found for the RT data.

Event Related Potential Data

Grand average waveforms for each VF condition are presented in Figure 2. The largest visual ERPs were observed in the P7 and P8 electrode pair, therefore analysis was

confined to this pair only. The eye movement grand average waveforms are shown in Figure 3. Deflections were observed in the eye tracks but these were minimal and cannot account for the deflections seen in electrodes P7 and P8. Only participants with P1 and N1 peaks visible within an 80ms window of the grand averages were included for analysis. A three-way ANOVA was performed with Visual Field (left or right) and Electrode (P7 or P8) as the within-subjects factors and Group (younger or older) as the between-subjects factor. This analysis was performed separately for the P1 and N1 ERP components. Means and standard deviations of the peak latencies are presented in Table 2 and corresponding IHTT estimates are presented in Table 3.

For P1 latencies there was a significant effect of VF, $F(1,23)=5.38$, $p=.03$, $\eta^2=.19$, such that stimuli presented in the RVF produced shorter latencies ($M=132.46$, $SD=31.80$) compared to LFV presentations ($M=138.65$, $SD=27.52$). There was a significant VF x Electrode interaction, $F(1,23)=214.29$, $p<.001$, $\eta^2=.19$, indicating that latencies were significantly longer over the ipsilateral compared to the contralateral electrode in response to stimuli presented unilaterally to one VF (Table 3). This is consistent with an IHTT estimate in the anatomically predicted direction. The VF x Electrode x Group interaction was also significant, $F(1,23)=5.33$, $p=.03$, $\eta^2=.19$, indicating that the IHTT for the older participants was significantly shorter than younger participants (Table 3). No other significant effects were found for the P1 component.

For N1 latencies there was a significant effect of Electrode, $F(1,23)=7.84$, $p=.01$, $\eta^2=.25$, such that P7 produced shorter latencies ($M=154.56$, $SD=53.87$) compared to P8 ($M=199.58$, $SD=22.20$). As with the P1 data, there was a significant VF x Electrode interaction, $F(1,23)=184.69$, $p<.001$, $\eta^2=.89$, again indicating that latencies were significantly longer over the ipsilateral compared to the contralateral electrode. However, this did not differ between the groups; VF x Electrode x Group interaction was not significant, $F(1,23)=.00$, $p=.992$, $\eta^2=.00$. No other significant effects were found for the N1 component.

Table 1. Mean Reaction Times (milliseconds) and Standard Deviations for Each Hand by Visual Field Condition and the Crossed-Uncrossed Difference for Each Visual Field in Younger and Older Participants

	Left Visual Field					Right Visual Field				
	Left Hand		Right Hand		CUD	Left Hand		Right Hand		CUD
	M	SD	M	SD	M	M	SD	M	SD	M
Younger	188.13	30.37	193.01	28.83	4.88	195.83	37.54	184.86	30.64	10.97
Older	180.64	37.41	184.14	32.10	3.50	185.42	37.05	177.41	33.49	8.01

Note: CUD = crossed-uncrossed-difference

Table 2. Mean P1 and N1 Latencies (milliseconds) Recorded by the P7 and P8 Electrodes for Each Visual Field in Younger and Older Participants

	Younger								Older							
	P1				N1				P1				N1			
	Contralateral		Ipsilateral		Contralateral		Ipsilateral		Contralateral		Ipsilateral		Contralateral		Ipsilateral	
	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD	M	SD
LVF	116.5	17.0	165.7		180.3	9.2	207.1	12.5	122.3	23.7	153.5	20.6	184.8	16.5	205.9	20.6
	9	7	6	12.9	8	3	3	8	3	8	8	9	9	5	5	9
RVF	101.9	17.0	156.0	15.9	170.1	10.	207.7		111.8	12.6	155.8	17.8	173.7		217.1	13.0
F	4	6	4	2	7	7	2	15.4	7	8	2	7	8	8.75	2	8

Note: LVF = left visual field; RVF = right visual field; P1 = the first positive ERP peak; N1 = the first negative ERP peak

Table 3. Averaged Interhemispheric Transfer Time (IHTT) Estimates for Younger and Older Participants

	CUD	ERP
Younger	7.93	41.89
Older	5.76	34.90
Total	6.85	38.40

Note: CUD = crossed-uncrossed-difference; ERP = Event related potential

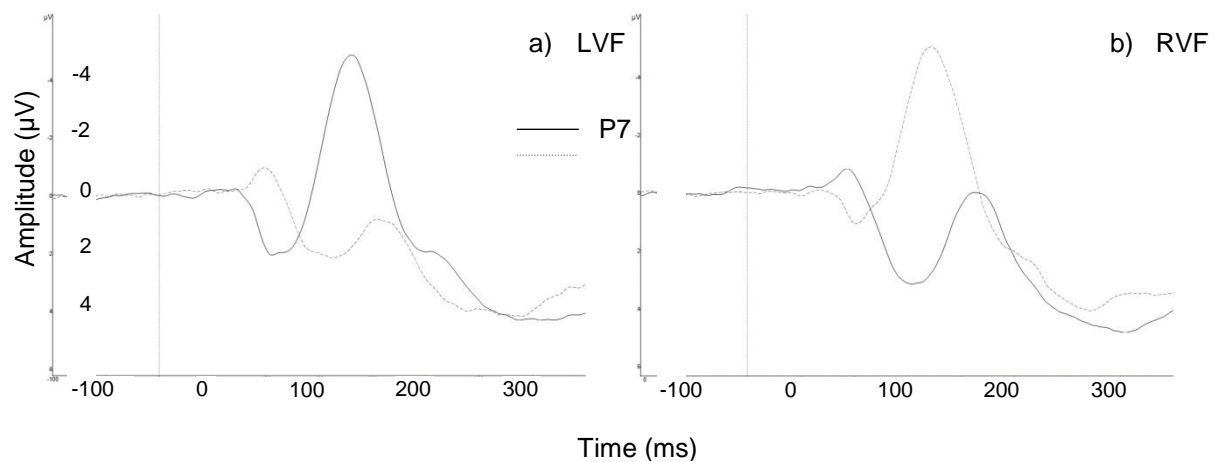


Figure 2. Grand average waveforms (N = 29) for a) left (LVF) and b) right visual field (RVF) stimuli. Amplitude expressed in microvolts (μV). P7 and P8 refer to left and right hemispheric electrode sites respectively.

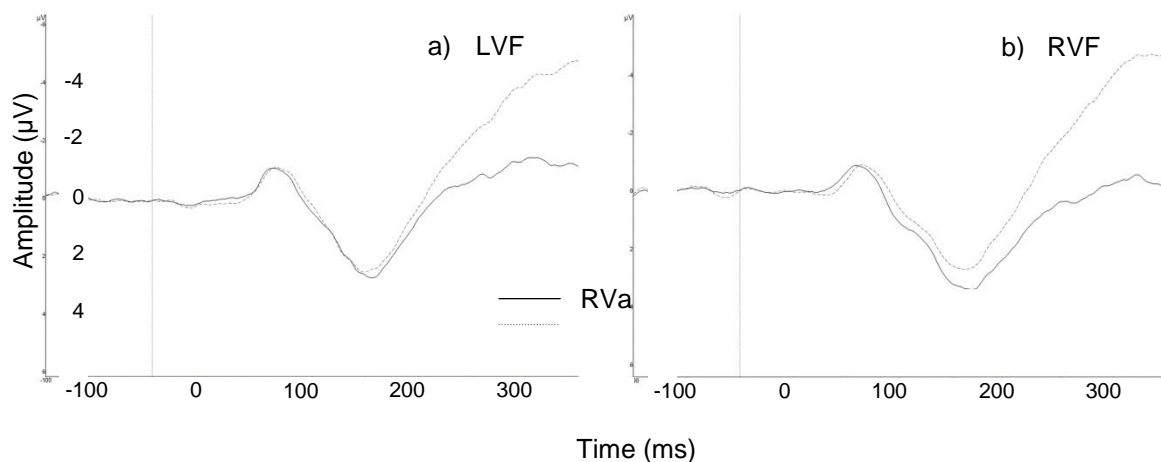


Figure 3. Grand average waveforms (N = 29) for the electrodes monitoring eye movements of the right eye for a) left (LVF) and b) right visual field (RVF) stimuli. Amplitude expressed in microvolts (μV). RVa and RVb refer to electrodes placed lateral to and below the right eye respectively.

Discussion

The main aim of this research was to investigate whether aging has an effect on interhemispheric transfer time (IHTT). It was predicted that IHTT would increase with age. However, results indicate that the older participants had a faster IHTT compared to the younger group, based on the P1 ERP component, which is contrary to the prediction. The RT results also show this trend, although results were not significant. These results also contrast with the literature which suggests IHTT either

increases with age (Curran, et al., 2001; Jeeves & Moes, 1996; Reuter-Lorenz & Stanczak, 2000; Schulte, et al., 2004), or does not change (Hoptman, et al., 1996; Linnet & Roser, 2012). However, as these results have not been found in prior studies, replication is required before firm conclusions can be made. The present work is therefore unable to disentangle the inconsistencies found in the literature therefore further research is needed. Future work may benefit from a focus on the stimuli used. Previous work investigating the effects of aging show a pattern with the behavioural CUD based experiments using a small white circular stimuli (Jeeves & Moes, 1996; Linnet & Roser, 2012; Reuter-Lorenz & Stanczak, 2000; Schulte, et al., 2004), whereas the ERP experiments used a checkerboard pattern (Hoptman, et al., 1996; Saron & Davidson, 1989). Despite evidence that adjusting visual properties of stimuli does not affect IHTT estimates (Braun, 1992; Corballis, 2002), it would be good practice for all studies to have a standardised procedure for such investigations to allow direct comparison.

A possible explanation for the present results could be the large proportion of female participants in the younger group. Research has suggested that females have a prolonged IHTT compared to males (Braun, 1992) which could explain the longer IHTT estimates found this group. However, the majority of studies fail to replicate this finding (Braun, Achim, & Larocque, 2003) and a more recent study has found the opposite pattern of results (Moes, Brown, & Minnema, 2007). Gender, therefore, cannot fully account for the differences found between the groups in this study. However, just as in Hoptman et al's (1996) study, due to the small male sample size (EEG data, N=3; RT data, N=7), statistical analysis was not used to compare the effect of gender on IHTT therefore conclusions cannot be made on its effect. Future research should control for gender in order to reduce the risk of this variable being a possible confound.

Another possible explanation for the results seen could be bilateral recruitment in the older but not younger participants aiding their performance (Grady, 2008). Grady (2008) indicates that areas of the prefrontal cortex are recruited by older but not younger participants in some tasks. The prefrontal cortex has been implicated in the Poffenberger paradigm (Iacoboni & Zaidel, 2004; Saron, et al., 2004). Reuter-Lorenz, Stanczak, and Miller (1999) found that bilateral recruitment is mediated by task complexity. Older adults were faster for the across-hemisphere processing condition for intermediate and high complexity tasks, whereas the younger participants showed this advantage only for the highest level of complexity. It was concluded that across-hemisphere processing was advantageous for older adults at lower levels of complexity than younger participants. In the present study this could account for the differences seen between the groups; if the older participants were aided by bilateral processing, this may have led to faster integration of information between the hemispheres and as such a faster IHTT. Cabeza, Anderson, Locantore, and McIntosh (2002) found bilateral recruitment for high but not low-performing older adults compared to younger participants, suggesting the higher the performance of older adults, the greater likelihood of bilateral activation. The older adults in the present study performed better than the younger participants and could be considered high-performers, again indicating that bilateral processing and recruitment could have aided performance. However, consistent with the work of Reuter-Lorenz, et al. (1999), Banich and colleagues (1990; 1998; 2000) conclude that simple tasks are better solved by one hemisphere, while complex tasks by two.

The Poffenberger paradigm is a simple reaction time task which may not be complex enough to elicit bilateral recruitment in older participants. Future research could investigate this through brain imaging methods with younger and older participants whilst completing the Poffenberger paradigm.

Bilateral recruitment, if applicable to this paradigm, could also account for the RT results of this study. Although not significant, the RT results indicate that the older participants had a faster reaction time than the younger participants. However, this again contrasts with the general understanding that reaction times slow with age (Jeeves & Moes, 1996; van der Knapp & van der Ham, 2011). However, as RT is a behavioural measure, another explanation could be that of the motivation of participants to perform well (Reips, 2000). The younger participants took part in the study in return for course credit which may have affected their willingness to perform as perhaps they felt they had to be there. The older participants, however, volunteered to take part in return for cash payment. This indicates that these participants wanted to take part and were therefore more likely to be motivated to perform well (Reips, 2000). Of further note is that the majority of these participants were not interested in the cash payment, providing some evidence of their intrinsic motivation to take part in the study. Externally motivating factors could also have had an affect such that the older participants may have been responding to demand characteristics of the study (Orne, 1962). They might have wanted to please the experimenter and provide the results they thought the experimenter wanted to find and therefore tried harder to respond more quickly. For future research it might be advisable for both younger and older participants to be recruited from outside of the university course credit scheme. Having both groups of participants recruited from the same population would reduce the risk of motivation being a confounding variable.

Both the CUD and ERP measures produced a significant IHTT in the anatomically predicted direction, with ERP measures producing longer estimates than the CUD measure which is consistent with the literature (Hoptman, et al., 1996; Saron & Davidson, 1989). Although the IHTT estimates found are within the range typically reported, they are slightly longer than expected. The participants in this study were instructed to respond using their thumbs, which according to Braun (1992) should have produced shorter CUDs than using the index finger. However, this was not the case in this study as using thumbs did not produce shorter CUDs.

The CUD estimates of IHTT indicate that stimuli presented to the LVF produce a shorter IHTT than RVF stimuli. This indicates an asymmetry of transfer times such that right-to-left hemispheric transfer is faster than left-to-right which is consistent with the literature (Barnett & Corballis, 2005; Marzi, et al., 1991). Due to the significant effects of VF and Electrode in the P1 and N1 results respectively, any directionality differences seen in the ERP data are confounded and therefore were not calculated. By collapsing the data across the P1 and N1 components, these confounds should be cancelled out and therefore the overall average IHTT estimate for the ERP measure can be relied upon. The RVF advantage seen in the P1 data is consistent with the findings of Jeeves & Moes (1996) who also found this advantage in their CUD data.

Another prediction of this study was that ERPs would be larger over occipital electrode sites compared to parietal sites. In fact, larger ERPs were visible in the ventrolateral electrode pair of P7 and P8. This result is consistent with Saron and Davidson's (1989) conclusion that lateral sites produce larger ERPs than medial occipital sites; although it should be noted that their study was based on sites over the parietal occipital lobe which are located more medially than P7 and P8 used in this study. An unexplored avenue in the present study was whether there were differences in the ERPs resulting from visual input and those related to the motor output. Iacoboni and Zaidel (2004) found areas of the superior parietal cortex to be involved in the CUD which they suggest is linked to response preparation. An investigation of response locked ERPs could shed light on this link and allow the study of timing of parietal response to see if it is in fact response preparation or perhaps performance.

Another unexplored avenue in this study was the finding of Hoptman, et al. (1996) that the quality of information transferred was reduced in older participants. Given the finding in the present study that older participants appear to have a faster transfer time than younger participants, it would be of interest to see how, or if, the amplitude of the waveforms over the ipsilateral hemisphere were affected. This could be achieved through additional analysis of the existing data, or given the limitations of this study (see below) by re-running the experiment. The latter of these options would also provide opportunity to see if these findings can be replicated, or if they are inimitable.

A limitation of this study is the number of trials completed by each participant of 300 experimental stimuli presentations. This level is consistent with the 280 trials used by Reuter-Lorenz and Stanczak (2000), although not with Saron and Davidson (1989) and Hoptman, et al. (1996) who used 400 trials and Westerhausen, et al. (2006) who used 600. The review by Braun (1992) indicates that although the number of trials does not appear to have any effect on CUD duration, larger numbers of trials might be more likely to find effects between groups. It is worth noting, however, that the effect sizes found in the current study are on par with those of Westerhausen, et al. (2006) who were the only ones to report eta squared values (effect sizes).

Another limitation of this study was the number of artefacts and the level of noise found in the EEG output. Eye movement was monitored by electrodes placed lateral to and below the right eye. Although, the deflections seen in these electrodes are relatively small and cannot account for the deflections seen in P7 and P8, they may still have had an impact. Due to the level of artefacts and noise in the EEG data, a more relaxed approach was taken to data rejection in order to maintain participant numbers; a more stringent analysis could have resulted in a less noisy dataset. Despite the approach taken, over a third of the participants had to be rejected from the ERP data analysis due to excessive artefacts or noise. Several factors may have contributed to this poor dataset. One such example is that data collection was performed by three researchers. This meant that although all followed the same general procedures for instructing participants and recording the data, minor differences in delivery of task instructions or in the monitoring of the live EEG output could have resulted in more artefacts and/or noise in the recording. To eliminate the researcher as a possible confound and source of error, future research might benefit from an inter-researcher test of reliability to ensure that all researchers monitor the live EEG output identically.

Conclusion

To conclude, the present study suggests that older participants have a faster interhemispheric transfer time than younger participants, based on the P1 ERP component. However, this result requires replication before firm conclusions can be made as it is contrary to the existing literature.

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